

Wildfire and Spruce Beetle Outbreak: Simulation of Interacting Disturbances in the Central Rocky Mountains

Author(s): R. Justin DeRose & James N. Long

Source: Ecoscience, 16(1):28-38. 2009.

Published By: Centre d'études nordiques, Université Laval

DOI: <http://dx.doi.org/10.2980/16-1-3160>

URL: <http://www.bioone.org/doi/full/10.2980/16-1-3160>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Wildfire and spruce beetle outbreak: Simulation of interacting disturbances in the central Rocky Mountains¹

R. Justin DEROSE² & James N. LONG, Department of Wildland Resources and Ecology Center, Utah State University, 5230 Old Main Hill, Logan, Utah 84322-5230, USA, e-mail: rjustinderose@gmail.com

Abstract: Infrequent large-scale natural disturbance regimes are an integral component of Engelmann spruce (*Picea engelmannii*) forests of the central Rocky Mountains. Wildfires, bark beetle outbreaks, winds, and avalanches cause relatively drastic changes in community structure, composition, and function. These disturbances may occur independently or interact where the incidence of one may change the potential for another. We assessed potential wildfire behaviour change in the wake of a catastrophic, landscape-wide spruce beetle (*Dendroctonus rufipennis*) outbreak in southern Utah, USA. Using data collected in spruce forests affected by the outbreak, the Forest Vegetation Simulator and Fire and Fuels Extension were used to simulate long-term (100 y) stand dynamics and potential fire behaviour under 3 reconstructed scenarios: no spruce beetle outbreak (low-severity), 50% spruce beetle-caused mortality (mid-severity), and 95% spruce beetle-caused mortality (high-severity). Simulations suggested a likely reduction in probability of active crown fire for 1 or 2 decades on near-pure Engelmann spruce sites after high-severity mortality. This counterintuitive result suggested extreme fire behaviour is not an inevitable consequence of spruce beetle outbreaks. No change in potential fire behaviour was predicted in stands with the least reduction in spruce basal area (low- or mid-severity). In one stand with a history of surface fire, stand structure and potential fire behaviour from low- and high-severity simulations were influenced by surface fire ~100 y ago. These results are indicative of complex disturbance interactions that were influenced by the host-specific spruce beetle, resultant stand structures and fuel profiles, and in one case antecedent disturbance.

Keywords: crowning index, extreme fire weather, flame length, fuel loading, fuel models, torching index.

Résumé : Des régimes de perturbations naturelles à grande échelle, peu fréquentes, sont une composante intégrale des forêts d'épinettes d'Engelmann (*Picea engelmannii*) du centre des montagnes Rocheuses. Les feux de forêts, les épidémies de coléoptères s'attaquant à l'écorce, le vent et les avalanches causent des changements relativement radicaux dans la structure, la composition et la fonction des communautés. Ces perturbations peuvent se produire de façon indépendante ou interagir entre elles de façon à ce que l'incidence de l'une puisse changer le potentiel de l'autre. Nous avons évalué le changement de comportement de feux potentiels à la suite d'une épidémie catastrophique à la grandeur du paysage du dendroctone de l'épinette (*Dendroctonus rufipennis*) dans le sud de l'Utah, États-Unis. En utilisant des données récoltées dans des pessières touchées par l'épidémie et le simulateur « Forest Vegetation Simulator incluant le Fire and Fuels Extension », une simulation à long terme (100 ans) de la dynamique des peuplements et du comportement de feux potentiels a été réalisée pour trois scénarios de reconstruction : aucune épidémie du dendroctone de l'épinette (faible sévérité), 50 % de mortalité causée par le dendroctone (sévérité moyenne) et 95 % de mortalité causée par le dendroctone (sévérité élevée). Les simulations ont suggéré une réduction probable de la probabilité de feu de cime actif pour une ou deux décennies après une mortalité de sévérité élevée dans des peuplements presque purs d'épinettes d'Engelmann. Ce résultat contraire à l'intuition suggère qu'un comportement extrême du feu n'est pas une conséquence inévitable des épidémies du dendroctone de l'épinette. Aucun changement du comportement de feux potentiels n'a été projeté dans les peuplements où l'aire basale des épinettes a été la moins réduite (sévérité faible ou moyenne). Dans un peuplement avec un historique de feu de surface, la structure du peuplement et le comportement de feux potentiels étaient influencés par un feu de surface datant d'environ 100 ans lors des simulations de sévérité faible et élevée. Ces résultats indiquent des interactions complexes entre les perturbations influencées par le dendroctone dont l'hôte spécifique est l'épinette, les structures de peuplement et les profils de carburant résultants et dans un cas, une précédente perturbation.

Mots-clés : conditions météorologiques extrêmement propices au feu, hauteur de la flamme, indice de feu de cime actif, indice d'inflammation, modèles de carburant, quantité de carburant.

Nomenclature: Wood, 1982; Flora of North America Editorial Committee, 1993.

Introduction

Large-scale disturbances are major ecosystem processes shaping community patterns in forested subalpine systems. Stand-replacing fire has received the most attention and is typically implicated as the primary disturbance factor for

subalpine forests of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) (Peet, 2000). Recently, however, the spruce beetle (*Dendroctonus rufipennis*) has been affecting large areas of Engelmann spruce forests across the western US and Alaska (Veblen *et al.*, 1991; Berg *et al.*, 2006; DeRose & Long, 2007). Epidemic populations of the spruce beetle dramatically affect community composition and structure, which, in turn, may influence community response to future disturbance (Baker & Veblen, 1990;

¹Rec. 2008-01-08; acc. 2008-07-04.

Associate Editor: Dominique Arseneault.

²Author for correspondence.

DOI 10.2980/16-1-3160

DeRose & Long, 2007). Increasingly, disturbance interactions have become a focus of interest in disturbance ecology (Veblen *et al.*, 1994; Schoennagel, Veblen & Romme, 2004; Kulakowski & Veblen, 2007). In particular, the change in fire behaviour in post-beetle outbreak forests is a topic of considerable interest (W. H. Romme, J. Clement, J. Hicke, D. Kulakowski, L. H. MacDonald, T. L. Schoennagel & T. T. Veblen, unpubl. data; M. O. Crawley, unpubl. data).

Multiple hypotheses of disturbance interactions for Engelmann spruce forests exist. However, there is little consensus concerning connections between extreme wildfires and spruce beetle outbreaks. For example, Bigler, Kulakowski, and Veblen (2005) provided evidence that in a severe 2002 fire in a subalpine forest in western Colorado, probability of severe fire was only slightly increased in areas affected by the 1940s spruce beetle outbreak; they found that those sections that had burned in the late 1800s, resulting in stand structures and cover types less susceptible to burning, had a strongly reduced extent of severe fire. Also in western Colorado, both watershed-scale (Veblen *et al.*, 1994; Kulakowski, Veblen & Bebi, 2003) and regional-scale (Bebi, Kulakowski & Veblen, 2003) analyses did not support the general expectation of increased fire occurrence following the 1940s spruce beetle outbreak that killed most mature Engelmann spruce in the White River National Forest (Schmid & Frye, 1977). Similarly, analysis of the extent and severity of 2002 fires in western Colorado in areas affected by the late 1990s spruce beetle outbreak (*i.e.*, during the red-needle and grey-needle phases) did not show an increase in either fire extent or severity in beetle-killed forests (Kulakowski & Veblen, 2007). Again, among variables related to stand conditions, stand origin following late 19th century fires was the strongest predictor of (reduced) fire extent. Although low-severity surface fires are not believed to be widespread in spruce–fir forests in Colorado, Kulakowski, Veblen, and Bebi (2003) found that the 1940s spruce beetle outbreak reduced stand susceptibility to low-severity fire, perhaps due to increased moisture in the forest floor. A more general pattern of severe fires creating young post-fire spruce–fir stands that mitigate against spruce beetle attack for at least 70 y has been widely documented in western Colorado (Veblen *et al.*, 1994; Kulakowski, Veblen

& Bebi, 2003; Kulakowski & Veblen, 2006). It is apparent that potential interactions between wildfires and spruce beetle outbreaks in Engelmann spruce forests are both complex and not completely understood (Jenkins *et al.*, 2008).

Forest composition and structure prior to a spruce beetle outbreak in combination with host-specific mortality influences the short-, mid-, and long-term changes in fuel profiles. A rapid decrease in foliar moisture content occurs in the short-term (2–3 y). More profound changes to canopy fuels occur in the mid-term (one to many decades) due to a reduction in live spruce density, which shifts the distribution of canopy foliage to subcanopy, non-host species (*e.g.*, aspen [*Populus tremuloides*]), and subalpine fir. As a result, both canopy base height (CBH) and canopy bulk density (CBD) are reduced. Longer-term (many decades to centuries) influences include the addition of beetle-killed trees to the surface fuel load and changes in CBH and CBD associated with the density, composition, and growth of the understory trees.

These changes in the fuel profile affect potential fire behaviour (Table I). Potential surface fire intensity and flame length will increase through time as dead trees enter the surface fuel pool. Passive crown fire behaviour where individual trees may “torch” (Scott & Reinhardt, 2001) is influenced by flame lengths and post-outbreak reductions in CBH. Torching is necessary to initiate active crown fire, which can be maintained if CBD is sufficient (Agee & Skinner, 2005). Alternatively, conditional fire behaviour occurs when CBD is sufficient for active crown fire but flame lengths are too low or CBH is too high for initiation of passive crown fire (Scott & Reinhardt, 2001). Potential fire behaviour associated with post-beetle outbreak changes in the fuel profile can be evaluated under extreme fire weather using 3 criteria (Reinhardt, Crookston & Rebain, 2003): 1) flame length, which indicates the intensity of surface fire and, in combination with CBH, whether passive crown fire behaviour is likely; 2) Torching index (TI, $\text{km}\cdot\text{h}^{-1}$), which is indicative of passive fire potential; and 3) Crowning index (CI, $\text{km}\cdot\text{h}^{-1}$), which is indicative of active crown fire potential.

We examined potential interactions between 2 extremely important types of disturbance in Engelmann spruce

TABLE I. Potential fire behaviour types, rules for their occurrence, and evaluation criteria under extreme fire weather used in this study, from Reinhardt, Crookston, and Rebain (2003).

Fire type	Description	Evaluation criteria
Surface	Flame length depends on fuel loading and fuel moisture content, spread influenced by slope and wind speed	Crowning index ^a and torching index ^b > critical wind speed ^c
Passive	“Torching” where individual trees or small groups of trees burn but solid flame is not maintained in the canopy, occurs when a critical wind speed is exceeded	Crowning index > critical wind speed and torching index < critical wind speed
Active	“Crowning” where both the surface and canopy burn, solid flame maintained from ground to canopy, occurs when a critical wind speed is exceeded	Crowning index and torching index < critical wind speed
Conditional	“Crowning” possible but limited by insufficient ladder fuels for surface fire to enter canopy	Crowning index < critical wind speed but torching index > critical wind speed

^a Crowning index is the wind speed necessary to maintain active crown fire.

^b Torching index is the wind speed necessary to ignite the canopy of individual trees.

^c Critical wind speed is a threshold value, determined from extreme fire weather, that indicates whether fire can move from the surface to the canopy.

forests. Fire behaviour predictions incorporate forecasts of stand dynamics to characterize the effects of changes in canopy and stand structure as a result of the spruce beetle outbreak. Three scenarios, representing different levels of spruce beetle impact, were developed to simulate potential fire behaviour across a range of Engelmann spruce stand structure, composition, and fuel loading. The first scenario simulated potential fire behaviour for mature Engelmann spruce forest structure with little to no spruce beetle-caused mortality (low-severity). The second scenario simulated the effect of changed canopy fuels as a result of a spruce beetle outbreak (high-severity, > 95% spruce mortality). The third scenario examined the effect of canopy fuels changes associated with intermediate levels of spruce beetle-caused mortality (mid-severity, ~50% spruce mortality). To explore interactions between disturbances we posed the question, is a high-severity spruce beetle outbreak likely to increase or decrease subsequent potential fire behaviour? Disturbance interactions were indicated by changes in potential fire behaviour as a result of the various levels of spruce beetle mortality and were based on modeled predictions of crowning and torching indices (Table I).

Methods

STUDY AREA

This study was conducted in high-elevation Engelmann spruce forests in the Dixie National Forest on the Markagunt Plateau (DeRose & Long, 2007), one of several southern Utah plateaus dissected by rivers draining the western edge of the greater Colorado Plateau. The Markagunt Plateau is ~20 km east of Cedar City, Utah, and the Engelmann spruce forests range from 2700 to 3300 m asl. In the early 1990s, endemic populations of spruce beetle built to incipient levels, and within a few years a full-blown outbreak was underway that eventually moved across the entire plateau. Engelmann spruce mortality was severe and shifted forest dominance to subalpine fir and aspen (DeRose & Long, 2007).

Winter snowfall from the west and summer monsoons from the southeast (Mock, 1996) bring bimodal annual precipitation to the Markagunt and other southwestern Utah plateaus (Aquarius, Paunsaugunt, Sevier). This distribution

of annual precipitation has likely had a large influence on historical fire occurrence (Figure 1).

Five study sites that were dominated by Engelmann spruce prior to the outbreak were studied (Table II). Ashdown, located just to the north of Cedar Breaks National Monument, and Snotel, just south, both had an understory of gooseberry (*Ribes montigenum*) and aspen bluebells (*Mertensia arizonica*). Bristlecone Pine Trail, Midway, and Navajo Lake, located southeast of Cedar Breaks, had minimal herbaceous vegetation. These sites represent a range of pre-outbreak Engelmann spruce composition, structure, and fuel loading (Tables II and III).

FIRE WEATHER AND FUEL MOISTURE

Wind speed, temperature, and fuel moisture associated with extreme fire weather were reconstructed using the local Remote Automated Weather Station (RAWS) historical weather data from Aqua Canyon for 1990–2006 (archived data at <http://fam.nwcg.gov/fam-web/weatherfirecd/utah.htm>) (Table IV). Fire Family Plus (<http://www.fire.org/>) was used to calculate wind speed, temperature, and fuel

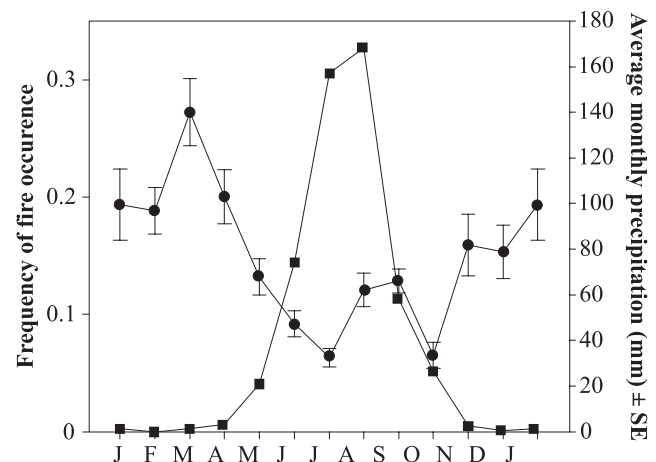


FIGURE 1. Average monthly precipitation (mm) \pm 1 SE (circles) for the Midway Valley Snowpack Telemetry (SNOTEL) site (37° 56' N, 112° 83' W, 2987 m elevation) from 1982 to 2005 and frequency of fires (squares) on the Cedar City Ranger District from 1970 to 2006. Fire frequency data from fire occurrence files for the Dixie National Forest (<http://fam.nwcg.gov/fam-web/weatherfirecd/utah.htm>).

TABLE II. Stand-level attributes of the 5 study sites.

Site	Latitude	Longitude	# plots	Approx. year of outbreak	Site index ^b (m)	Average slope (%)	Elevation (m asl)	Species composition ^a (percent basal area)						
								ES (PD)	ES (RD)	ES (L)	SF	AS	DF	LM
Ashdown	37° 66'	112° 84'	6	1996	13.4	2.5	3197	< 1	78	8	14	-	-	-
Bristlecone Pine Trail	37° 56'	112° 85'	4	1999	15.2	28	3016	< 1	65	3	8	-	22	2
Midway	37° 56'	112° 79'	10	1999	16.7	2	2977	< 1	62	3	11	24	-	-
Navajo Lake	37° 52'	112° 81'	6	2000	17.6	21	2846	2	39	9	20	-	28	2
Snotel	37° 59'	112° 86'	5	1998	16.1	24	3229	3	86	3	8	-	-	-

^a Species composition at time of 2006 measurement, including live (L), recently dead Engelmann spruce (RD), and pre-outbreak Engelmann spruce snags (PD), but not including standing dead of other species. ES = Engelmann spruce; SF = subalpine fir; AS = aspen; DF = Douglas-fir; LM = limber pine.

^b Site index base age 50 y.

TABLE III. Surface fuel loading ($\text{Mg}\cdot\text{ha}^{-1}$), designated fuel model, and associated weights for each site on the Markagunt Plateau.

Site	0–0.64 (cm)	0.65–2.54 (cm)	2.55–7.62 (cm)	> 7.63 (cm) sound	> 7.63 (cm) rotten	Fuel bed depth (cm)	Fuel model ^a	Fuel model weight (percent)
Ashdown	0.76	4.53	10.9	3.6	35.1	17	2 / SB1	30 / 70
Bristlecone Pine Trail	2.13	6.43	8.3	23.6	20.5	6	SB1	100
Midway	1.57	6.41	8.1	20.8	23.9	10	TU5 / SB1	50 / 50
Navajo Lake	0.72	3.38	6.3	24.6	20.6	15	SB1	100
Snotel	0.38	5.89	3.2	2.8	48.2	7	2 / SB1	30 / 70

^a Fuel model as defined by Albini (1976) and Scott and Burgan (2005).

TABLE IV. Fuel moisture content and fire weather data used for potential fire behaviour modeling under extreme weather (97th percentile) in the Fire and Fuels Extension.

	97 th percentile
1 h	1.9
10 h	2.1
100 h	3.2
1000 h	4.9
Live herbaceous	29.7
Live woody	60
Dry bulb temperature (°C)	28
Maximum probable 1-m wind speed ($\text{km}\cdot\text{h}^{-1}$)	39

moisture content associated with historical extreme weather (97th percentile). One-min wind speed gusts were estimated from RAWS 10-min sustained wind speed measurements using NOAA tables (<http://www.wrh.noaa.gov/slc/projects/wxcalc/wxcalc.php>).

CANOPY, UNDERSTORY, AND SURFACE FUEL MEASUREMENTS

Between 4 and 10 prism plots (basal area factor = $3.0 - 8.0 \text{ m}^2$, held constant for each site; Bell & Dilworth, 2002) at least 100 m apart were measured on a grid pattern established with a randomly located starting point. On each plot every tree was recorded for species, status (alive, dead, and cause of mortality), diameter at breast height (DBH, 1.3 m), height (HT), and height to the base of the live crown (CBH). For the spruce beetle-killed Engelmann spruce trees, CBH was estimated based on the height at which fine branches were retained. Special care was taken to differentiate whether an Engelmann spruce had been killed by the recent spruce beetle outbreak, past spruce beetle mortality, or another agent. Recent mortality was noted by the presence of beetle galleries and sloughing bark, whereas past beetle mortality was indicated by beetle galleries on grey boles and the general absence of bark. Other agents were identified by the absence of spruce beetle galleries. Increment cores taken to the pith at 5–30 cm above ground level were returned to the lab and processed using standard core preparation techniques (Stokes & Smiley, 1968). Conservative estimates of age and 10-y diameter increment were determined by counting rings. Slope, aspect, and elevation were recorded for each plot.

At the centre of each prism plot a 2-m-radius fixed-area subplot was delineated, and every tree less than 5 cm DBH was identified by species and measured for HT and diameter at the root collar. These understory trees were sectioned at ground level, taken to the lab, and processed using standard preparation techniques (Stokes & Smiley, 1968). Conservative estimates of age were determined by counting rings.

Surface fuel loading included all dead woody debris and was tallied by diameter classes at each plot (see below) using the planar transect method (Brown, Oberheu & Johnston, 1982) (Table III). One-h and 10-h fuels were measured along a 2-m transect, and 100-h fuels on a 4-m transect. All debris > 7.63 cm (1000+ h moisture time-lag, coarse woody debris [CWD]) was measured along a 30-m transect. Species and condition (sound or rotten) were noted when discernable. Fuel bed depth, height of the tallest surface fuel up to 2 m, was measured at 3 points along each transect. Duff depth and litter depth were measured every 3 m along each transect (10 times). Five digital photographs per plot were taken to complement the fuel transects when identifying fuel models. Fuels Management AnalystTM (Carlton, 2006) was used to reduce surface fuel data to appropriate classes for model input (Table III).

DATA ANALYSIS

We explored possible interactions between spruce beetle outbreaks and subsequent fire using field-collected data to parameterize models of forest stand dynamics and fire and fuel behaviour. The Forest Vegetation Simulator (FVS) and its Fire and Fuels Extension (FFE) allow multi-year predictions of stand and fuel dynamics and potential fire behaviour. All data were imported into FVS for analysis and modeling. FVS is a deterministic, distance-independent, individual-tree growth and yield model developed from region- and species-specific allometric equations (Crookston & Dixon, 2005). In FVS, density-related tree mortality is predicted using relative stand density index, whereas density-independent mortality must be invoked by the user, e.g., with FFE. FVS is able to calibrate HT and large-tree diameter growth with measurements of HT, crown ratio ($[\text{HT} - \text{CBH}]/\text{HT}$), site index, and 10-y diameter increment (Dixon, 2002). Site index (an integrative measure of site quality based on height and age of dominant trees) was calculated from 6 dominant Engelmann spruce from each site (Alexander, 1967). Regeneration does not occur automatically in FVS; rather, it relies on user-supplied data input at appropriate time steps. Understory stocking and age data were used to estimate past natural regeneration by species and 10-y age classes; these estimates were used by FVS to simulate future regeneration for each site. Site-level analyses were performed using data averaged across plots.

FFE is an integrative fire behaviour model incorporating surface fire models (Rothermel, 1972), crown fire initiation models (Van Wagner, 1977), and representative fuel models (Albini, 1976; Anderson, 1982; Scott & Burgan, 2005) to simulate natural and prescribed fire behaviour.

FFE combines stand growth simulation data from FVS with fuel data to make predictions of potential fire behaviour (Reinhardt, Crookston & Rebas, 2003) (Table I). After every cycle of growth in FVS, stand-level data are handed-off to FFE, which updates fuel profiles (Johnson, Peterson & Raymond, 2007). For example, if tree mortality occurs during a simulation, this will be reflected in calculations of CBD and CBH by FFE. However, FFE does not take into consideration the red-needle stage of beetle outbreaks, where dry needles remain on the tree. Likewise, variations in wind speed associated with stand density are not explicitly considered by FFE. Similarly, canopy foliar moisture is not directly considered; CBD is used instead. The model can be enhanced with user-defined variables for fuel loading, fire weather, and rate of snag fall. Measurements of surface fuel are not used directly for fire behaviour predictions. Rather, they are used to define one of the fuel models (see below, Scott & Burgan, 2005); users can specify a combination of fuel models. Neither FVS nor FFE take explicit consideration of herbaceous and grass growth and associated fuel loading; instead, fire behaviour predictions are driven by overstory and understory trees and fuel models.

Stand dynamics and potential fire behaviour were evaluated for 3 scenarios of spruce mortality: 1) a low-severity scenario reconstructed from field data represented forest conditions immediately prior to the 1990s spruce beetle outbreak, including trees killed prior to the recent outbreak; 2) a high-severity scenario characterized forest conditions 6-10 y following the spruce beetle outbreak; and 3) an alternative reconstructed scenario represented a mid-severity outbreak with ~50% mortality. Forest structure for the low-severity scenario was recreated by changing the status of all Engelmann spruce killed by the recent spruce beetle outbreak to live. Field data were used to simulate the high-severity scenario (~95% spruce mortality) (DeRose & Long, 2007). The mid-severity scenario was created by modifying the reconstructed low-severity data to reflect 50% mortality of large-diameter Engelmann spruce, consistent with the spruce beetle literature (Schmid & Frye, 1977; Holsten, *et al.*, 1999). Since the outbreak was recent (Table II), small changes in fire behaviour as a result of changes in diameter increment of live trees post-outbreak are inconsequential. Increased fuel bed depth as a result of the spruce mortality is likely for 2-3 y post outbreak; however, very little needle litter was observed on fuel transects, which suggests rapid needle decomposition. Virtually all the Engelmann spruce killed in the outbreak were still standing.

FUEL MODELS

Fuel models integrate surface fuel load, bulk density, and moisture of extinction in a mathematical representation for fire behaviour predictions, *e.g.*, FFE (Scott & Burgan, 2005). These simplified fuel models allow the use of Rothermel's (1972) fire spread equations. As a result, fire behaviour models are highly influenced by fine fuels, whereas the amount of CWD has little effect on initial fire spread: grass, shrubs, or herbaceous plants will affect fire spread more than CWD. The 11 fuel models originally identified by Rothermel (1972) were subsequently improved by Albini (1976) and most recently enhanced by Scott and

Burgan (2005). These fuel models describe fuel characteristics during the most extreme periods of the fire season (Anderson, 1982). We used the newly developed fuel models of Scott and Burgan (2005) and 1 of the original models from Anderson (1982) in this study since these, used in combination, are most likely to accurately predict surface fire characteristics. We used plot photos and surface fuel loading estimates (Table III) to determine the major carrier of fire, *e.g.*, herbaceous, shrub, conifer litter, *etc.*, and defined site-specific fuel models (Scott & Burgan, 2005).

FIRE MODELING

All fire simulations were run with FVS/FFE for 100 y. For each scenario, we evaluated the predicted fire behaviour under extreme fire weather conditions (*i.e.*, wind speed, fuel moistures, air temperature, and humidity at the 97th percentile). The primary difference between the scenarios was the number of dead Engelmann spruce modeled as live. We only reconstructed Engelmann spruce trees determined to have been killed by the spruce beetle during the recent outbreak. Therefore, stands in the low-severity scenario included a small percentage of standing dead spruce previously killed by spruce beetle or another agent (Table II). Slopes of fuel transects were averaged over all plots for FFE input. The SnagFall keyword was used to simulate the rate of snag fall based on observations in southern Utah, *i.e.*, ~0.6% per year (Mielke, 1950). FFE default values of shrub and herbaceous fuel loading were used. The temperature, wind speed, and fuel moistures associated with extreme fire weather (Table IV) were entered into FFE.

Results

LOW-SEVERITY SCENARIO

Results from the low-severity scenario indicated torching and crowning were possible throughout the 100-y simulation in all stands but 1 (Bristlecone Pine Trail, see below) (Figure 2a) and with the exception of 1 decade (2026) in which conditional fire behaviour was predicted for another stand (Snotel). Torching and crowning are likely when TI and CI are predicted to be below the critical wind speed threshold (Table I). Predicted torching and crowning were promoted by the high CBD associated with live canopy foliage (Figure 3a) coupled with the low CBH characteristic of substantial ladder fuels (Figure 3b) and sufficiently long FL (Figure 3c) for surface fire to enter the canopy. Thus, with the exception of the Bristlecone Pine Trail stand (see second-order disturbance interaction below), spruce stand structures in the low-severity scenario were associated with the potential for crown fire on all sites throughout the simulations (Figure 2a).

MID-SEVERITY SCENARIO

Similarities in CBD, CBH, and FL between the low- and mid-severity scenarios (Figure 3) suggested little difference in predicted fire behaviour (Figure 2a-b). Like the low-severity scenario, the mid-severity scenario showed the potential for torching and crowning throughout the simulation on all sites except Bristlecone Pine Trail (Figure 2b), with the exception of 2 decades (2086 and 2096) in which conditional fire behaviour was predicted for Snotel. Conditional fire behaviour occurs when crowning is likely but torching is not (Table I).

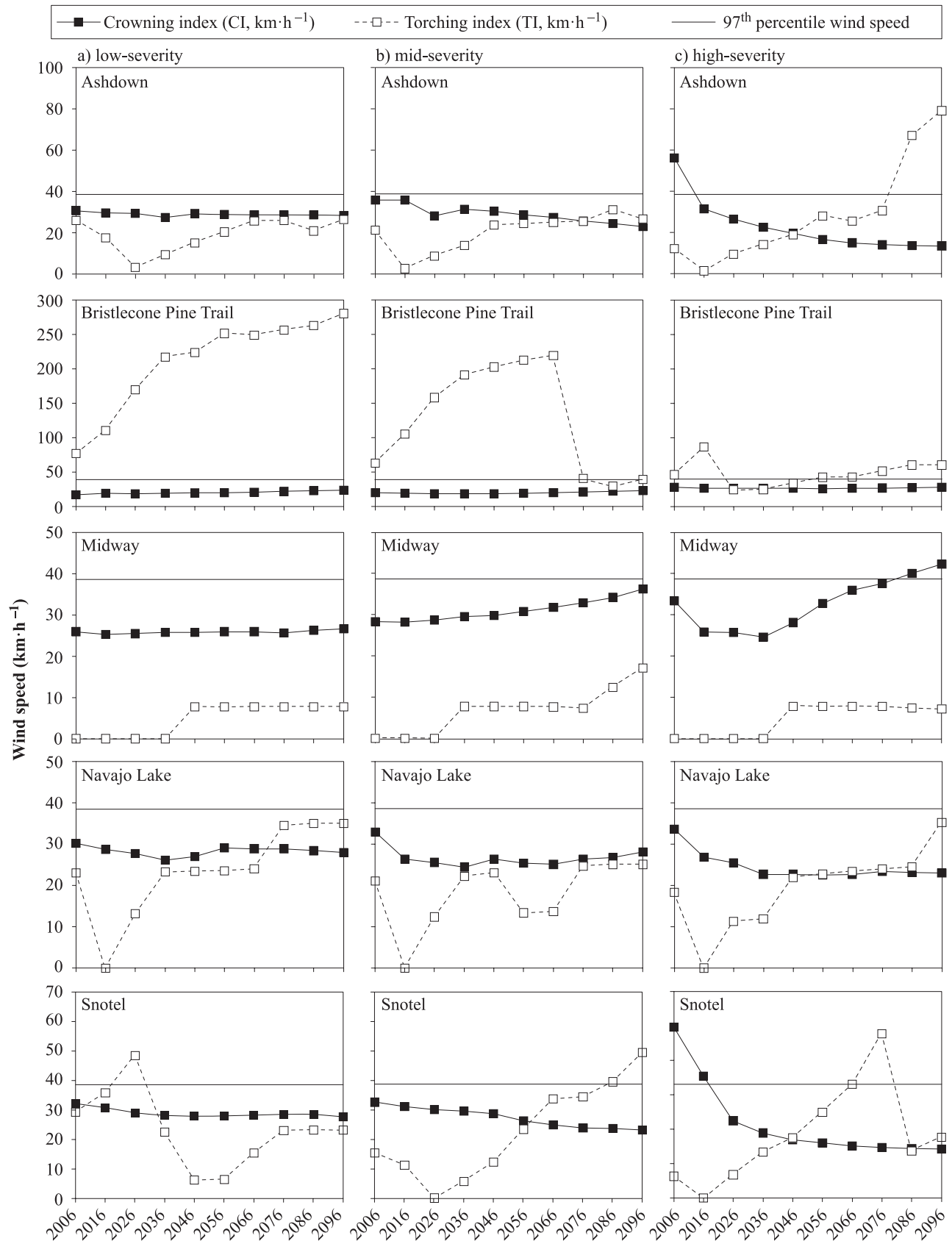


FIGURE 2. Crowning and torching indices ($\text{km}\cdot\text{h}^{-1}$) over the simulation period for the study sites under a) endemic spruce beetle scenario, b) epidemic spruce beetle scenario, and c) post-epidemic spruce beetle scenario. Values above the 97th percentile wind speed (solid horizontal line) indicate unlikely torching or crowning. Values below indicate torching or crowning likely.

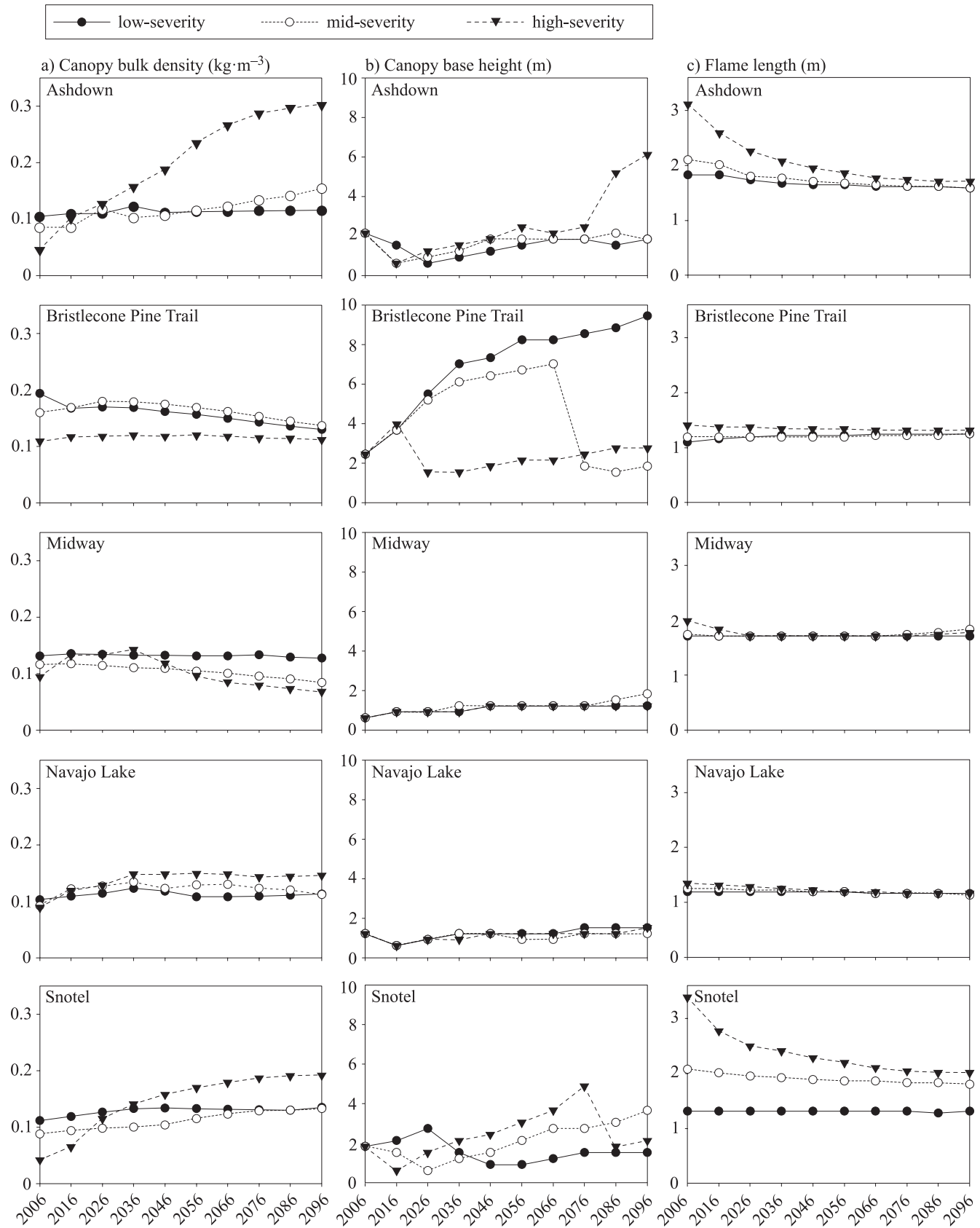


FIGURE 3. Canopy bulk density ($\text{kg}\cdot\text{m}^{-3}$) (a), canopy base height (m) (b), and flame length (m) (c) by site under each scenario (low-, mid-, and high-severity) for the simulation period (2006–2096).

HIGH-SEVERITY SCENARIO

For the high-severity scenario only sites with relatively pure Engelmann spruce composition resulted in reduced TI and CI for a couple of decades (Ashdown and Snotel, Figure 2c, Table II). Therefore, a threshold in spruce composition exists beyond which a high-severity beetle outbreak may actually result in reduced crown fire behaviour. Below this threshold, low- to mid- to high-severity comparisons of CBD, CBH, and FL (Figure 3) revealed little difference between scenarios for Midway and Navajo Lake. Both sites exhibited crowning and torching fire behaviour regardless of the spruce mortality scenario. Therefore, a lower percentage of spruce composition prior to an outbreak resulted in little change in potential fire behaviour between low- and high-severity spruce beetle mortality.

SECOND-ORDER DISTURBANCE INTERACTION

In an unusual case, forest structure at Bristlecone Pine Trail influenced the 1990s beetle outbreak but not scenarios of low- or high-severity fire behaviour. Conditional fire behaviour was predicted for both the low- and mid-severity scenarios except for the 3 final decades (2076–2096) in the mid-severity scenario, where torching was possible. Low TI values (Figure 2) were likely due to regenerating trees and associated fuel loading, which resulted in a gradual reduction of CBH. Crowning is unlikely in the high-severity scenario, but for 2026–2046 torching is possible, probably associated with reduced CBH in 2026 (Figure 3b). Even under extreme weather it is likely that only a surface fire would occur on Bristlecone Pine Trail due to the combination of high CBH and low FL (Figures 3b–c). Bristlecone Pine Trail had sufficient CBD to maintain a crown fire for the low- and mid-severity scenarios (Figure 3); however, extremely high CBH (Figure 3b) suggested crowning is unlikely. In the high-severity scenario a combination of relatively low CBH and relatively long FL would indicate the possibility for crown fire; however, drastic reduction in CBD due to the severe spruce mortality associated with this scenario suggests only surface fire is likely.

Discussion

LOW-SEVERITY SCENARIO

Pre-outbreak (low-severity scenario) Engelmann spruce forest structure and species composition influenced predictions of fire behaviour. Bigler, Kulakowski, and Veblen (2005) found that the probability of high-severity fires after spruce beetle outbreaks was highly influenced by stand structure (young versus old), which is not inconsistent with our results. In general, pre-outbreak (low-severity) mature Engelmann spruce forests are much more likely to exhibit torching and crowning under extreme fire weather conditions, as a result of their relatively continuous horizontal and vertical fuel distribution (except for Bristlecone Pine Trail).

MID-SEVERITY SCENARIO

Predictions of fire behaviour under the mid-severity scenario were not intermediate to the low- and high-severity scenarios but rather deviated only slightly from the low-severity scenario (Figure 2). The relatively diverse composition in Midway and Navajo Lake resulted in smaller

differences in CBD, such that crowning and torching fire behaviour were likely regardless of spruce mortality (low-, mid-, or high-severity). Furthermore, a dense understory of aspen and subalpine fir ensured that CI and TI stayed below the critical wind speed threshold throughout the simulations (Figure 2). Similarly, the modeled understory regeneration accentuated the vertical canopy structure and ensured consistently high CBD and low CBH (Figure 3a–b), both of which exacerbated torching and crowning.

HIGH-SEVERITY SCENARIO

Extreme fire behaviour is not an inevitable consequence of spruce beetle epidemics. Under the high-severity scenario, our simulations predicted reduced crown fire behaviour (high CI and TI) for stands that had relatively pure spruce composition prior to the outbreak (Ashdown and Snotel, Table II). This counterintuitive result was likely driven by substantial reductions in CBD (Figure 3a) associated with the host-specific spruce beetle outbreak. Even though severe spruce mortality in relatively pure stands “looks” more flammable, the Ashdown and Snotel stands under the high-severity scenario had few residual live trees, a reduction in horizontal crown continuity, and an understory of primarily herbaceous plants, which resulted in many decades of reduced crown fire behaviour. Under these conditions, surface fire is possible, but crown fire is unlikely, even under extreme weather conditions, until substantial regeneration develops. Consistent with our results, Bebi, Kulakowski, and Veblen (2003) found low-elevation subalpine forests were not more susceptible to subsequent fire than areas without a history of spruce beetle outbreak. Similarly, Kulakowski, Veblen, and Bebi (2003) found that low-severity fires post-beetle outbreak were much more common in stands with < 19% beetle mortality, whereas stands with > 60% mortality had fewer fires than expected. This is similar to the results from our high-severity scenario for Ashdown and Snotel, which had > 95% spruce mortality and reduced crown fire behaviour. High-severity simulations showed mid-term (2–3 decades) crowning is unlikely in Ashdown (2006) and Snotel (2006–2016). However, after 4–5 decades, development of a regenerating understory (increasing CBD, Figure 3a) resulted in a decrease in both TI and CI, increasing the likelihood of active crown fire. Furthermore, long FL for both sites, a result of the increased herbaceous fuel loading, resulted in the possibility of torching for the first 6 or 7 decades of the simulation (Figure 3).

SECOND-ORDER DISTURBANCE INTERACTION

Bristlecone Pine Trail was an unusual example of a fire by spruce beetle by potential fire disturbance interaction. A human-ignited surface fire occurred on this site *ca.* 1906 (J. Bowns, pers. comm.). Increment cores extracted from recently killed Engelmann spruce at Bristlecone Pine Trail corroborated that spruce regeneration followed the 1906 surface fire. Veblen *et al.* (1994), Bebi, Kulakowski, and Veblen (2003), and Kulakowski and Veblen (2006) documented a reduction in susceptibility to spruce beetle outbreak as a result of antecedent stand-replacing fires, where the youngest stands (~50 y) were the least susceptible. Although Bristlecone Pine Trail burned in 1906, the fire was not stand-replacing and likely acted only to reduce

surface fuels and kill smaller trees while leaving many larger Douglas fir and limber pine. Unfortunately, even the relatively young (~100 y old) spruce were entirely killed in the recent outbreak; the *ca.* 70-y threshold before spruce are susceptible to the spruce beetle suggested by Veblen *et al.* (1994) for Colorado Engelmann spruce forests may also apply to southern Utah forests. The primary difference between Bristlecone Pine Trail and the other sites appears to be the death of understory trees and herbaceous species. The loss of understory trees to fire in 1906 resulted in a much higher CBH (Figure 3) even after 100 y, which undoubtedly contributes to the unlikelihood of torching at Bristlecone Pine Trail. Therefore, the 1906 surface fire reduced understory stocking and ladder fuels, which resulted in spruce regeneration that after ~100 y was susceptible to the beetle outbreak; however, it was the initial reduction in understory stocking and ladder fuels, not the outbreak *per se*, that influenced fire behaviour predictions. This provides evidence for a second-order disturbance interaction.

FVS / FFE MODELING CHALLENGES

The increase in herbaceous fuel loading following bark beetle outbreaks found in many forest types (McCambridge, Morris & Edminster, 1982; Holsten, Werner & Develice, 1995; Stone & Wolfe, 1996; McMillin & Allen, 2003) was also evident in Ashdown and Snotel. To account for the higher FL associated with increase in herbaceous species during modeling, a combination of fuel models was used (Table III). We simulated each stand with a 30% contribution from fuel model 2, which has relatively longer flame lengths than fuel model SB1. This resulted in longer FL early in the simulations (Figure 3c). Failure to take into account the increased herbaceous loading during simulations would have resulted in increased CI and TI for many more decades. Similarly, recent work in lodgepole pine stands suggested that fine fuel loading < 5 y after mountain pine beetle (*Dendroctonus ponderosae*) outbreaks increased significantly, purportedly due to needle and twig drop, and that this increase could lead to increased rates of spread and surface fire intensity (Page & Jenkins, 2007a,b). While it is possible our estimates of fine fuel were influenced by the recent needle drop associated with the outbreak (*i.e.*, 6–10 y prior), needles were not readily apparent on fuel transects. Furthermore, fuel transect data were not used directly for fire modeling (see Data analysis above), but rather their distribution across diameter classes was used, in part, to identify appropriate fuel models. Based on our surface fuel loading (Table III), it is unlikely that an increase in fine fuels would lead to the assignment of different fuel models.

Another modeling challenge associated with FFE is that it does not take into account the relatively short-duration of foliage retention post-outbreak (*e.g.*, 2–3 y for Engelmann spruce; Holsten *et al.*, 1999). Potential fire behaviour might spike during this short window, mostly due to decreased moisture in the crown. On the Markagunt Plateau, there were no severe fires during the short time between the spruce beetle attack and the complete loss of needles and fine branches (Fire occurrence data: <http://fam.nwccg.gov/fam-web/weatherfired/utah.htm>). Similarly, Kulakowski

and Veblen (2007) did not find support for greater fire severity 2–3 y after spruce beetle attacks. This short window likely represents the only time when crown fire might be more likely, given extreme fire weather, in pure Engelmann spruce sites affected by a high-severity beetle outbreak (*e.g.*, Ashdown or Snotel).

POTENTIAL FIRE, FUELS, AND WEATHER

Given enough time it is possible for extreme fire weather, ignition, and sufficient fuels to occur simultaneously, resulting in extreme fire behaviour in these Engelmann spruce forests. Past occurrence of small natural and human-caused fires on the Markagunt Plateau was primarily during the driest season, prior to summer monsoons (Figure 1). It is likely that this landscape has been without extreme, large-scale fire for many centuries (DeRose & Long, 2007). Although charcoal is ubiquitous on the plateau, the amount found varied by site (R. J. Deroose & J. N. Long, unpubl. data), and it could be many thousands of years old, possibly influenced by young lava flows (*ca.* 1000–3000 y BP; Moore *et al.*, 2004). A study of bog sediments from lower-elevation, mixed-conifer forests on the Markagunt Plateau suggested an average fire return interval of 330–410 y (Madsen *et al.*, 2002), but this localized analysis may not characterize higher-elevation Engelmann spruce-dominated forests. It is clear that the fuel loading necessary for crown fire existed prior to the outbreak (low-severity scenario) and in some cases after the outbreak. Therefore, extreme fire weather and ignition must be limiting the occurrence of fire in this system. Bessie and Johnson (1995) found that both surface fire intensity and crown fire initiation were more strongly related to extreme fire weather than to fuel loading in subalpine forests, and Sibold, Veblen, and Gonzalez (2006) and Schoennagel *et al.* (2007) found evidence for this in Colorado. We found that extreme fire weather is necessary for burning on the Markagunt Plateau, but critical thresholds for fuel loading and stand structure must also be met. It appears that, in general, the change in fuel profiles and species composition between pre-outbreak (low-severity) and post-outbreak (high-severity) forests on the Markagunt Plateau does not always result in increased potential fire behaviour. Instead, on some sites (*i.e.*, Ashdown and Snotel) a counterintuitive effect, reduced potential fire behaviour, was the result.

Conclusion

Model simulations suggested pre-outbreak (low-severity) Engelmann spruce forest structure and composition influenced the spruce beetle outbreak, which subsequently affected predicted fire behaviour on the Markagunt Plateau in southern Utah. Interactions between the outbreak and subsequent potential fire behaviour were related to Engelmann spruce composition: 1) at sites with lower spruce composition (Midway and Navajo Lake), the spruce beetle outbreak did not change canopy structure sufficiently to alter the potential for crown fire; 2) at sites with high spruce composition (Ashdown and Snotel), the host-specific spruce beetle substantially reduced canopy fuel and therefore subsequent crowning potential for at least several decades; and 3) in 1 site with a known surface fire history (Bristlecone

Pine Trail), the influence of the beetle outbreak on canopy fuel load may have had little or no net effect on subsequent potential fire behaviour, indicating a second-order disturbance interaction. Our results are consistent with interactions of spruce beetle and subsequent fire behaviour, with the results heavily influenced by pre-outbreak Engelmann spruce composition. We conclude that extreme fire behaviour is not an inevitable consequence of spruce beetle outbreaks.

Acknowledgements

This paper was presented as part of the International Union of Forest Research Organizations–Società Italiana di Selvicoltura ed Ecologia Forestale–sponsored International Conference: Natural Hazards and Natural Disturbances in Mountain Forests, Sept. 2007 in Trento, Italy. We wish to acknowledge the Ecology Center and the T. W. Daniel Endowment for support of this study. This research was supported in part by the Utah Agricultural Experiment Station, Utah State University, Logan, Utah. Approved as journal paper no. 7946. We thank B. Bentz and two other reviewers for providing thoughtful comments that substantially improved this paper.

Literature cited

- Agee, J. K. & C. N. Skinner, 2005. Basic principles of forest fuel reduction treatments. *Forest Ecology and Management*, 211: 83–96.
- Albini, F. A., 1976. Estimating Wildfire Behavior and Effects. USDA Forest Service General Technical Report GTR-INT-30, Ogden, Utah.
- Alexander, R. R., 1967. Site Indexes for Engelmann Spruce in the Central Rocky Mountains. USDA Forest Service Research Paper RMRS-RM-32, Fort Collins, Colorado.
- Anderson, H. E., 1982. Aids to Determining Fuel Models for Estimating Fire Behavior. USDA Forest Service General Technical Report GTR-INT-122, Ogden, Utah.
- Baker, W. L. & T. T. Veblen, 1990. Spruce beetles and fires in the 19th-century sub-alpine forests of western Colorado, USA. *Arctic and Alpine Research*, 22: 65–80.
- Bebi, P., D. Kulakowski & T. T. Veblen, 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. *Ecology*, 84: 362–371.
- Bell, J. F. & J. R. Dilworth, 2002. Log Scaling and Timber Cruising. Oregon State University, Corvallis, Oregon.
- Berg, E. E., D. J. Henry, C. L. Fastie, A. D. De Volder & S. M. Matsuoka, 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management*, 227: 219–232.
- Bessie, W. C. & E. A. Johnson, 1995. The relative importance of fuels and weather on fire behavior in sub-alpine forests. *Ecology*, 76: 747–762.
- Bigler, C., D. Kulakowski & T. T. Veblen, 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. *Ecology*, 86: 3018–3029.
- Brown, J. K., R. D. Oberheu & C. M. Johnston, 1982. Handbook for Inventorying Surface Fuels and Biomass in the Interior West. USDA Forest Service General Technical Report GTR-INT-129, Ogden, Utah.
- Carlton, D., 2006. Fuels Management Analyst Plus Software, Version 3.0.2. Fire Program Solutions LLC, Sandy, Oregon.
- Crookston, N. L. & G. E. Dixon, 2005. The Forest Vegetation Simulator: A review of its structure, content, and applications. *Computers and Electronics in Agriculture*, 49: 60–80.
- DeRose, R. J. & J. N. Long, 2007. Disturbance, structure, and composition: Spruce beetle and Engelmann spruce forests on the Markagunt Plateau, Utah. *Forest Ecology and Management*, 244: 16–23.
- Dixon, G. E., 2002. Essential FVS: A User's Guide to the Forest Vegetation Simulator. Internal Report, USDA Forest Service, Fort Collins, Colorado.
- Flora of North America Editorial Committee, 1993-. *Flora of North America North of Mexico*. New York and Oxford.
- Holsten, E. H., R. A. Werner & R. L. Develice, 1995. Effects of a spruce beetle (Coleoptera: Scolytidae) outbreak and fire on Lutz spruce in Alaska. *Environmental Entomology* 24: 1539–1547.
- Holsten, E. H., R. W. Their, A. S. Munson & K. E. Gibson, 1999. The Spruce Beetle. USDA Forest Service, Forest Insect and Disease Leaflet 127, Washington, DC.
- Jenkins, M. J., E. Hebertson, W. Page & C. A. Jorgensen, 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management*, 254: 16–34.
- Johnson, M. C., D. L. Peterson & C. L. Raymond, 2007. Managing forest structure and fire hazard: A tool for planners. *Journal of Forestry* 105: 77–83.
- Kulakowski, D. & T. T. Veblen, 2006. The effect of fires on susceptibility of subalpine forests to a 19th century spruce beetle outbreak in western Colorado. *Canadian Journal of Forest Research*, 36: 2974–2982.
- Kulakowski, D. & T. T. Veblen, 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology*, 88: 759–769.
- Kulakowski, D., T. T. Veblen & P. Bebi, 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. *Journal of Biogeography*, 30: 1445–1456.
- Madsen, D. B., S. A. Elias, W. Chengyu, S. T. Jackson, R. S. Thompson & D. Rhode, 2002. The Paleocology of Red Valley Bog, Markagunt Plateau, Utah. Technical Report, National Park Service, USFS, Environmental Science, Utah Geologic Survey 32, Salt Lake City, Utah.
- McCambridge, W. F., M. J. Morris & C. B. Edminster, 1982. Herbage Production Under Ponderosa Pine Killed by the Mountain Pine Beetle in Colorado. USDA Forest Service, RMRS Research Note RM-416, Fort Collins, Colorado.
- McMillin, J. D. & K. K. Allen, 2003. Effects of Douglas-fir beetle (Coleoptera: Scolytidae) infestations on forest overstory and understory conditions in western Wyoming. *Western North American Naturalist*, 63: 498–506.
- Mielke, J. L., 1950. Rate of deterioration of beetle-killed Engelmann spruce. *Journal of Forestry*, 12: 882–888.
- Mock, C. J., 1996. Climatic controls and spatial variations of precipitation in the western United States. *Journal of Climate*, 9: 1111–1125.
- Moore, D. W., L. D. Nealey, P. D. Rowley, S. C. Hatfield, D. J. Maxwell & E. Mitchell, 2004. Geologic map of the Navajo Lake 7.5' quadrangle, Kane and Iron counties, Utah.
- Page, W. G. & M. J. Jenkins, 2007a. Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the Intermountain region. *Forest Science*, 53: 507–518.
- Page, W. G. & M. J. Jenkins, 2007b. Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. *Forest Science*, 53: 662–674.

- Peet, R. K., 2000. Forests and meadows of the Rocky Mountains. Pages 75–121 in M. G. Barbour & W. D. Billings (eds.). North American Terrestrial Vegetation. 2nd Edition, Cambridge University Press, Cambridge.
- Reinhardt, E. D., N. L. Crookston & S. A. Rebaun, 2003. The Fire and Fuels Extension to the Forest Vegetation Simulator and Addendum. USDA Forest Service RMRS-GTR 116, Ogden, Utah.
- Rothermel, R. C., 1972. A Mathematical Model for Predicting Fire Spread in Wildland Fuels. USDA Forest Service Research Paper INT-115, Ogden, Utah.
- Schmid, J. M. & R. H. Frye, 1977. Spruce Beetle in the Rockies. USDA Forest Service General Technical Report GTR-RM-49, Fort Collins, Colorado.
- Schoennagel, T., T. T. Veblen & W. H. Romme, 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience*, 54: 661–676.
- Schoennagel, T., T. T. Veblen, D. Kulakowski & A. Holz, 2007. Multidecadal climate variability and climate interactions affect subalpine fire occurrence, Western Colorado (USA). *Ecology*, 88: 2891–2902.
- Scott, J. H. & R. E. Burgan, 2005. Standard Fire Behavior Models: A Comprehensive Set for Use with Rothermel's Surface Fire Spread Model. USDA Forest Service RMRS-GTR-153, Fort Collins, Colorado.
- Scott, J. H. & E. D. Reinhardt, 2001. Assessing crown fire potential by linking models of surface and crown fire behavior. USDA Forest Service RMRS-RP-29, Fort Collins, Colorado.
- Sibold, J. S., T. T. Veblen & M. E. Gonzalez, 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. *Journal of Biogeography*, 33: 631–647.
- Stokes, M. A. & T. L. Smiley, 1968. An Introduction to Tree-Ring Dating. University of Chicago Press, Chicago, Illinois.
- Stone, W. E. & M. L. Wolfe, 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. *Vegetatio*, 122: 1–12.
- Van Wagner, C. E., 1977. Conditions for the start and spread of crown fire. *Canadian Journal of Forest Research*, 7: 23–34.
- Veblen, T. T., K. S. Hadley, M. S. Reid & A. J. Rebertus, 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology*, 72: 213–231.
- Veblen, T. T., K. S. Hadley, E. M. Nel, T. Kitzberger, M. Reid & R. Villalba, 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *Journal of Ecology*, 82: 125–135.
- Wood, S. L., 1982. The bark and *Ambrosia* beetles of north and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs*, 6: 1359.